

## EFFECT OF VARYING CARBOHYDRATE LEVELS ON THE UPTAKE AND TRANSLOCATION OF $^{32}\text{P}$ IN *ERAGROSTIS CURVULA* (SCHRAD.) NEES

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### ABSTRACT

The uptake and subsequent translocation of  $^{32}\text{P}$  among root, crown and leaf tissues of *Eragrostis curvula* were investigated in plants with varying carbohydrate levels. Plants were depleted of carbohydrates by being subjected to 3 days of continuous darkness and by defoliation. Plant roots were introduced to nutrient solutions containing  $^{32}\text{P}$ , at 0, 3, 6, 9, 12, 15 and 21 days after the depletion treatments. Initially, plants depleted of carbohydrates absorbed and translocated less  $^{32}\text{P}$  than the controls. Subsequently, uptake and translocation increased probably to restore the pools of phosphate to levels prior to the depletion treatments. Increased  $^{32}\text{P}$  uptake and translocation were related to an adequate supply of reserve carbohydrates.

### UITTREKSEL

DIE UITWERKING VAN WISSELENDE KOOLHIDRAATGEHALTE OP DIE OPNAME EN TRANSLOKASIE VAN  $^{32}\text{P}$  IN *ERAGROSTIS CURVULA* (SCHRAD.) NEES

Die opname en daaropvolgende translokasie van  $^{32}\text{P}$  in wortel-, kroon- en blaarweefsels van *Eragrostis curvula* is ondersoek by plante met verskillende koolhidraatgehalte. Die plante se koolhidrate is uitgeput deur ontblaring en blootstelling aan donkerte vir drie dae. Plantwortels is vir 0, 3, 6, 9, 12, 15 en 21 dae na die uitputtings-behandeling in voedingsoplossings wat slegs  $^{32}\text{P}$  bevat het, geplaas. Aanvanklik het die plante, waarvan die koolhidraatgehalte gedeeltelik uitgeput is, minder  $^{32}\text{P}$  as die kontroleplante geabsorbeer en getranslokeer. Daarna het opname en translokasie toegeneem, waarskynlik om die fosfaatpoele aan te vul tot die vlakke voor die uitputtings-behandeling. Verhoogde  $^{32}\text{P}$  opname en translokasie was afhanklik van 'n toereikende voorraad reserwe-koolhidrate.

### INTRODUCTION

Under grazing conditions grasses are frequently subjected to stress, chiefly as a result of defoliation and drought. Studies on the phosphorus nutrition of South African grasses under stress are limited. Knowledge of the trends in phosphorus uptake would yield information on the adoption of correct cutting and grazing practices and on the timing of fertilizer applications to pastures deficient in phosphorus.

*Eragrostis curvula* was selected for this study chiefly because of its agronomic importance as a pasture grass in South Africa. The uptake and distribution of phosphorus in plants have been the subject of many labelling experiments using  $^{32}\text{P}$  (Ahmad, 1963; Davis & Wareing, 1965; Loughman, 1966; Etter, 1967; Crossett, 1968). However, the effect of stress conditions on phosphorus uptake has

received little attention (Tarila, Ormrod & Adedipe, 1977). The objective of this study was to bring the plant under stress by depleting carbohydrates and to determine its effect on uptake and subsequent translocation of  $^{32}\text{P}$ .

## METHOD

### *Plant growth*

*Eragrostis curvula* (cv. Ermelo) plants were grown from seed in 150 mm clay pots containing a sterilised sandy loam soil. The plants were grown in an air-conditioned glasshouse. Following emergence seedlings were thinned and kept moist by frequent watering and periodic additions of a complete nutrient solution (Hoagland & Arnon, 1950). After 3 weeks seedlings were transferred to growth tanks containing complete nutrient solution. The growth tanks were continuously aerated and the solution level maintained by adding new nutrient solution. Solutions were renewed weekly.

### *Carbohydrate depletion treatments*

Four weeks after transfer to nutrient solutions plants were selected for uniformity, transferred to growth cabinets and subjected to one of two treatments for 3 days. In the control treatment, temperatures were maintained at 30 °C (day) and 15 °C (night), with a daylength of 12 h. In the second treatment plants were grown under the same temperature conditions as the control, but were maintained in complete darkness. At the end of the treatment period 50 % of the plants in each treatment were defoliated to a height of 30 mm above soil level. All plants were subsequently returned to control conditions and divided into four treatment groups. These were: control-uncut (C-U), control-cut (C-C), dark-uncut (D-U) and dark-cut (D-C).

The experimental design was a randomised complete block with two replications per treatment.

### *Labelling*

Two plants from each of the four treatments were labelled with  $^{32}\text{P}$  at 0, 3, 6, 9, 12, 15 and 21 days after completion of the carbohydrate depletion treatments. Plant roots were introduced to nutrient solutions containing  $^{32}\text{P}$  (40  $\mu\text{C}/500\text{ ml}$ ) as orthophosphate for 8 h.

### *Total nonstructural carbohydrates (TNC)*

Two plants from each of the four treatments were harvested for TNC determination on each harvest date. Plants were separated into roots and crowns, freeze-dried, weighed and ground to pass a 40 mesh screen. Carbohydrate determinations were made on 0.3 g samples according to the procedure of Smith (1969).

### Radioassay

Labelled plant roots were washed in running water to remove adhering radioactive solution. The plants were divided into roots, crowns, leaves and dried at 70 °C for 20 h. The plant parts were ground to pass a 40 mesh screen and 0,5 g samples wet ashed (Jackson, 1958). Aliquots of the ashed sample were pipetted onto glass fibre discs, dried under an infra-red lamp and placed in polyethylene counting vials containing 1 ml of scintillator. The scintillator used was toluene with two fluors, PPO and POPOP. All samples were counted in a Beckman LS-100 Liquid Scintillation System. All counts were corrected for background and for radioactive decay.

### Statistical analyses

Analyses of variance and F tests were applied to data obtained. When significant differences were detected treatment means were compared by Duncan's Multiple Range Test at the 5 % probability level. Correlation coefficients were calculated between TNC and total plant  $^{32}\text{P}$ .

## RESULTS AND DISCUSSION

### Carbohydrate analysis

The trends in percentage TNC in the roots (Fig. 1) and in the crowns (Fig. 2) were similar. Plants grown undisturbed in the dark for 3 days showed significant decreases in percentage TNC in roots and crowns on day 0. Root TNC in intact plants maintained in darkness (D-U) declined from 1,28 % initially to 0,34 % on day 0 representing a loss of 73 % (Fig. 1). The decline in TNC in the dark was due to the utilization of carbohydrates in respiration and growth. Thereafter, root TNC increased steadily since carbohydrate production was in excess of plant requirements. After day 0 there were no significant differences in root TNC of intact plants (C-U and D-U). Effects of the dark treatment on TNC in the crowns (Fig. 2) were similar to those of the roots. In the crowns of the D-U treatment TNC declined significantly from 3,65 % initially to 0,74 % on day 0, representing a loss of 80 %.

Defoliation resulted in significant decreases in TNC in the roots (Fig. 1) and crowns (Fig. 2) of the C-C treatments on day 3. Decrease in TNC continued till day 6 for the D-C treatment and up to day 9 for the C-C treatment. In the roots of the C-C treatment, TNC decreased from 1,34 % on day 0 to a minimum of 0,5 % on day 9 representing a loss of 63 % (Fig. 1). In the crowns (Fig. 2) defoliation resulted in a 76 % loss in TNC by day 9. There were no significant differences between TNC in roots or crowns of the D-C and C-C treatments after day 0. Defoliation did not have a marked effect on TNC in roots or crowns of the D-C treatment because of the very low pre-defoliation level of carbohydrate reserves.

The decrease in TNC following defoliation was presumably due to the utilization of carbohydrate reserves in regrowth and respiration. Although May &

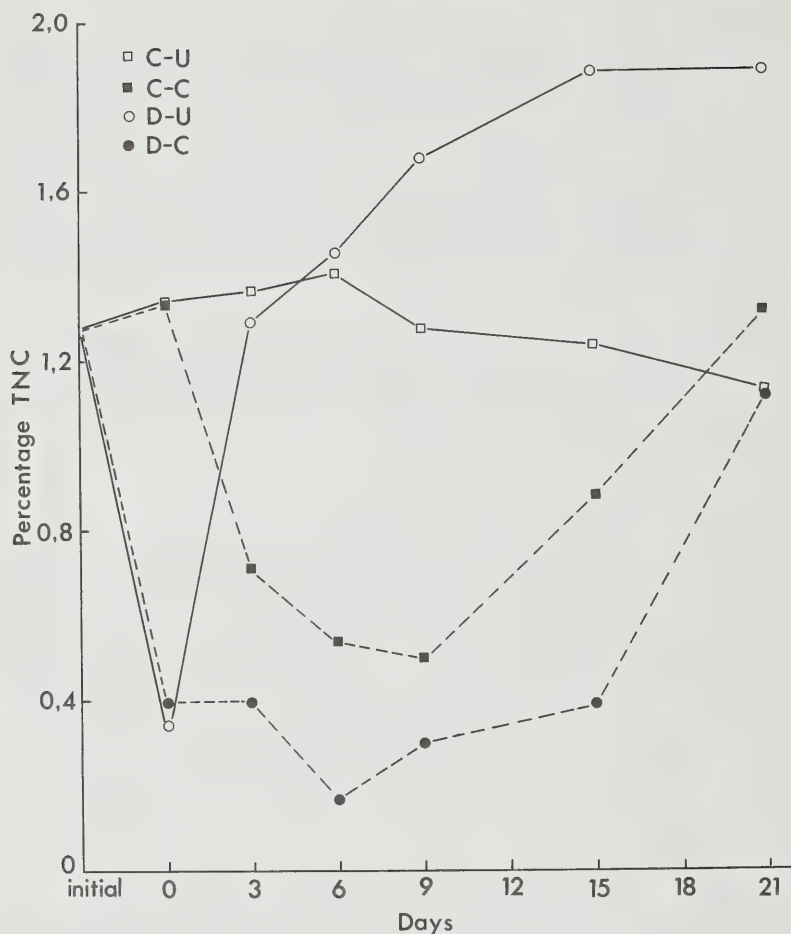


Fig.1. Changes in mean percentage TNC in the roots following treatments

Davidson (1958) queried the role of reserves in regrowth, results of several workers (Alberda, 1966; Steinke & Booysen, 1968; Steinke 1969) suggest that initial regrowth is dependent to a large extent upon an adequate supply of reserve carbohydrates. Percentage TNC in roots and crowns of defoliated plants continued to decrease as long as the production of photosynthetic assimilates fell short of the

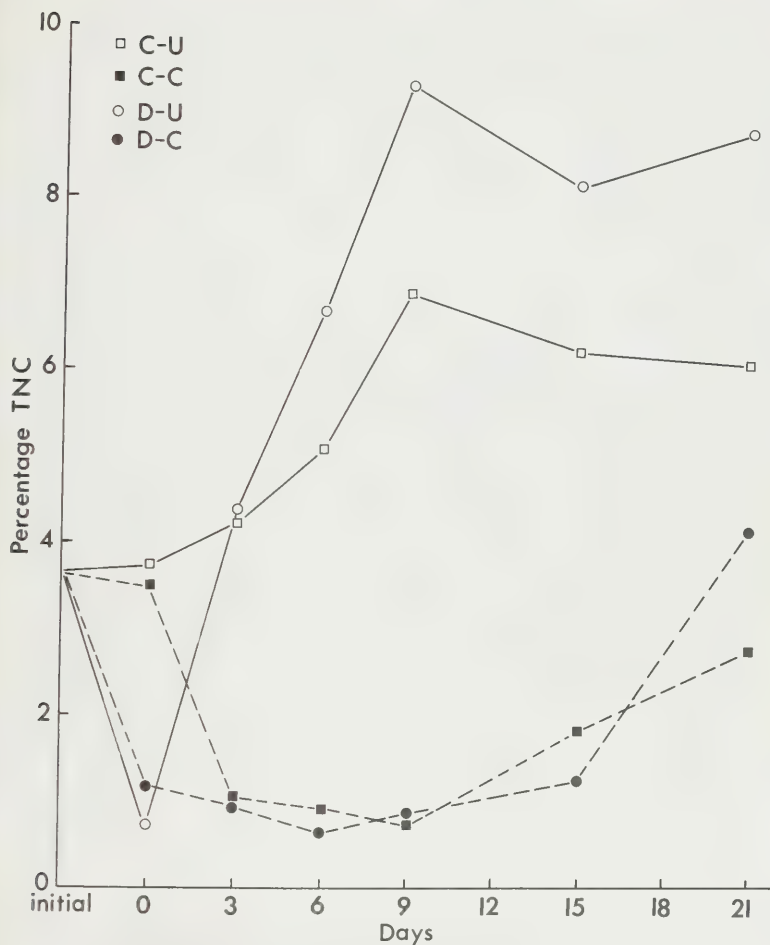


Fig.2. Changes in mean percentage TNC in the crowns following treatments

plant's requirements. This decrease was followed by a period of gradual recovery up to the end of 3 weeks. This increase indicates that sufficient leaf area had been produced so that production of assimilates by current photosynthesis was in excess of the plant's demand.

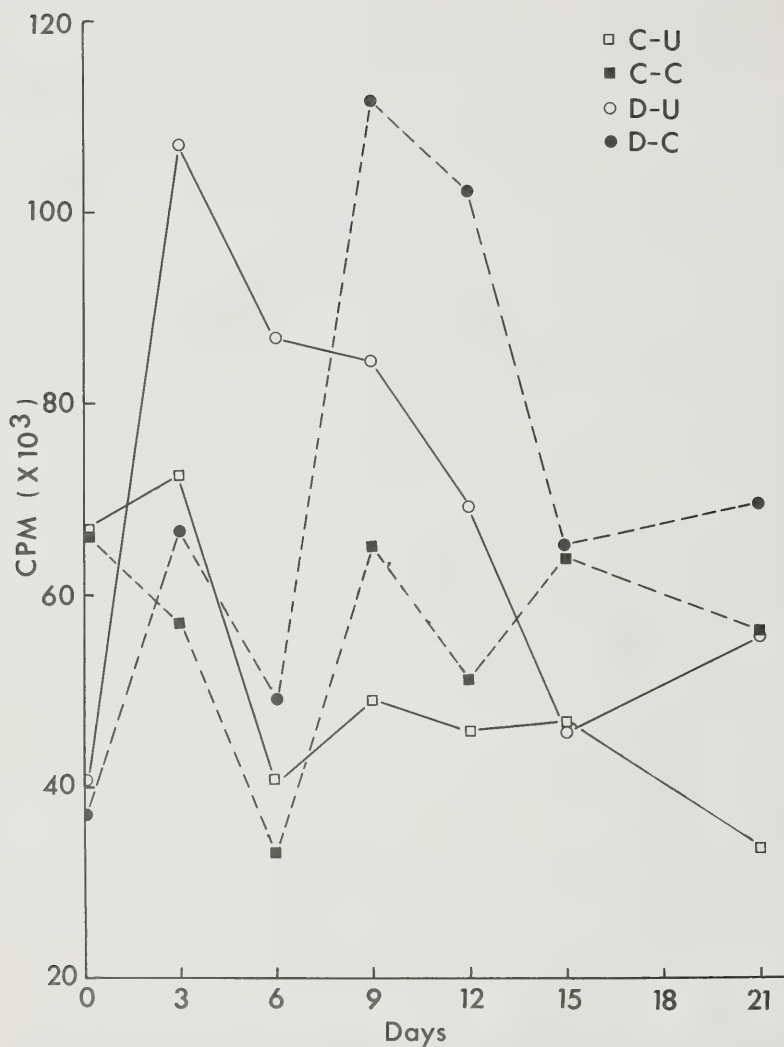


Fig.3. Changes in total plant  $^{32}\text{P}$  following treatments.

Trends in dry mass of roots and crowns for the various treatments were similar to those of percentage TNC and are therefore not presented.

Plants depleted of carbohydrates by the dark treatment absorbed significantly less  $^{32}\text{P}$  than the control plants on day 0 (Fig. 3).

Lower phosphate absorption by plants depleted of carbohydrates could probably be attributed to the lack of sufficient carbohydrate reserves for active uptake (Fig. 1). That reserve carbohydrates played an important role in phosphate uptake was further suggested by significant correlations between root TNC and total plant  $^{32}\text{P}$ .

Intact plants from the dark treatment (D-U) translocated significantly lower proportions of  $^{32}\text{P}$  to the crowns and leaves than the corresponding control treatment (C-U) on day 0 (Figs 4, 5 & 6). For example, in the C-U treatment 5.42% of the label was located in the crown and 3.18% in the leaves. In the D-U treatment 1.7% of the labelled phosphate was located in the crown and 0.57% in the leaves. In the crowns of defoliated plants (Fig. 5) the D-C treatment had significantly lower  $^{32}\text{P}$  (1.38%) than the C-C treatment (8.05%).

The rate of  $^{32}\text{P}$  uptake decreased when plants were maintained in darkness (results not presented). Plants maintained in darkness for 3 days were probably lower in phosphate than those that were illuminated. Differential phosphorus uptake by phosphorus-stressed maize plants was also demonstrated by Clark & Brown (1974). Reduced phosphate translocation to crowns of dark-treated plants on day 0 was probably due to the rapid incorporation of phosphate into organic compounds in the roots. That such rapid incorporation occurs in roots that are low in phosphate was demonstrated by Russel & Martin (1953), Ahmad (1963) and Loughman (1966). Rapid incorporation of  $^{32}\text{P}$  in roots that are low in phosphate is in agreement with the view that scarce metabolites are usually supplied to tissues nearest the source in preference to those further away.

The  $^{32}\text{P}$  content of the leaves of defoliated plants on day 0 was significantly higher than those of the intact plants. During the 8 h labelling period sufficient regrowth had occurred in defoliated plants to create active sinks for phosphate.

Uptake of  $^{32}\text{P}$  in the dark treatments (D-U and D-C) increased rapidly on day 3 (Fig. 3). In the D-U treatment maximum uptake occurred on day 3. In the D-C treatment uptake of  $^{32}\text{P}$  reached a maximum on day 9. Increased  $^{32}\text{P}$  absorption in the dark treatments was probably due to the restoration of phosphate pools to levels prior to the dark treatment. The energy requirements for active uptake were provided by the increasing levels of carbohydrate during the recovery period (Fig. 1). After the maximum had been obtained there was a decline in  $^{32}\text{P}$  uptake (Fig. 3). The drop in  $^{32}\text{P}$  uptake for all treatments on day 6 (Fig. 3) was due to an electrical failure during which time the temperature and light intensity were considerably reduced.

After day 0 trends in  $^{32}\text{P}$  distribution among roots, crowns and leaves of intact plants were similar. In defoliated plants a major portion of the phosphate was



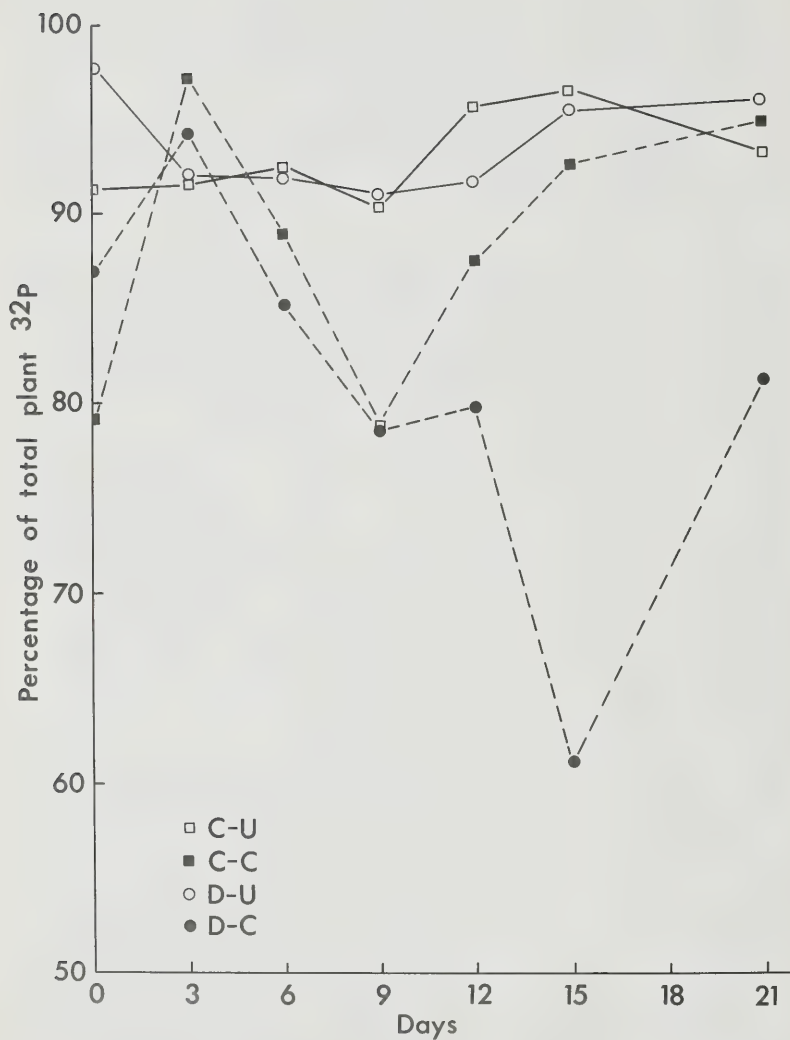


Fig.4. Changes in percentage of total plant  $^{32}\text{P}$  in the roots following treatments.



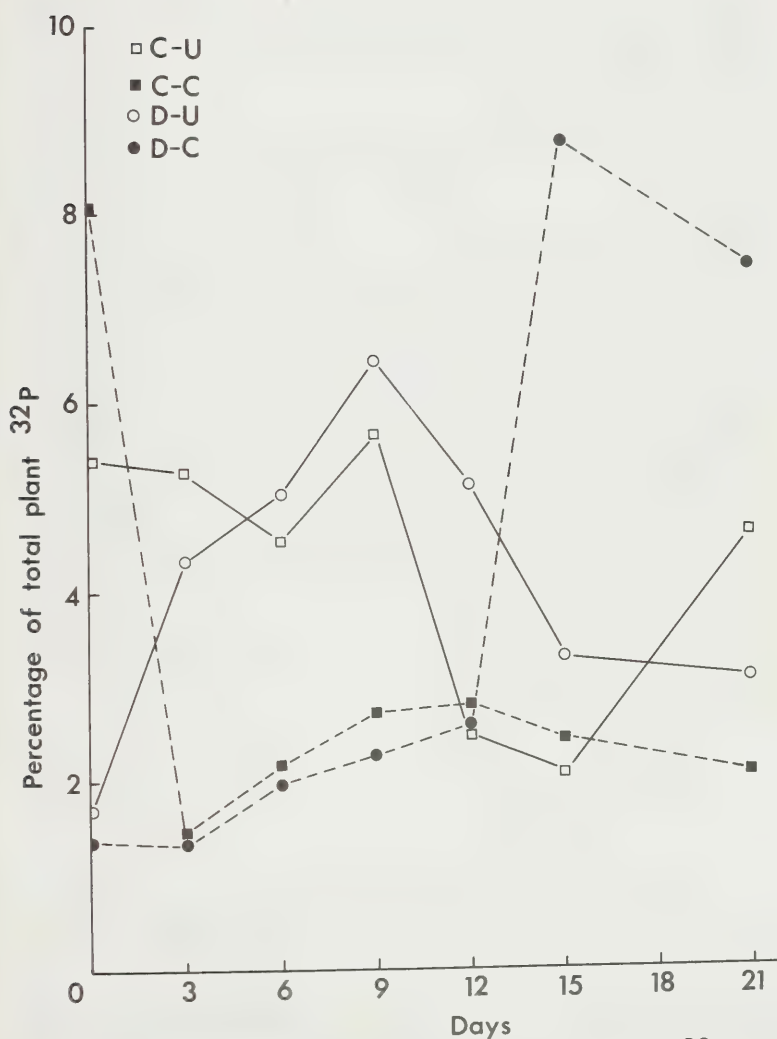


Fig.5. Changes in percentage of total plant  $^{32}\text{P}$  in the crowns following treatments

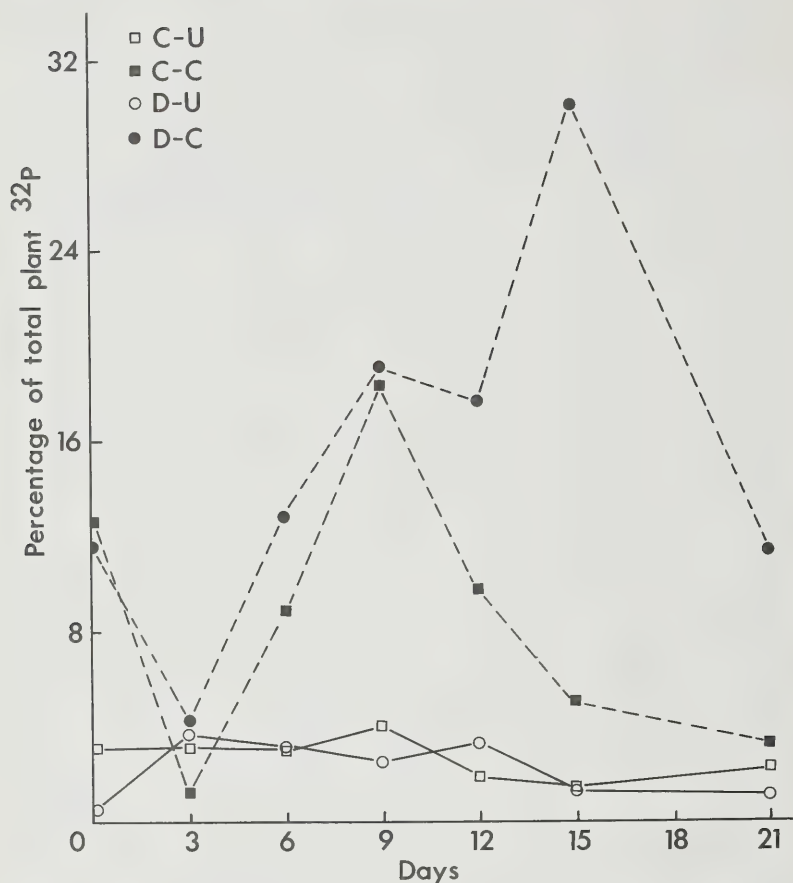


Fig.6. Changes in percentage of total plant  $^{32}\text{P}$  in the leaves following treatments

retained within the roots on day 3 probably as a result of the effect of defoliation in depleting carbohydrate reserves (Figs 1 & 2). Thereafter there was a rapid increase in translocation of  $^{32}\text{P}$  to the leaves as a result of rapid regrowth.

This study has revealed definite trends in phosphorus nutrition in plants under carbohydrate stress. Decrease in phosphate uptake during the dark treatment was followed by a rapid increase upon reillumination. This seems to suggest that the

rapid  $^{32}\text{P}$  uptake in light was probably a response to restore the pools of phosphate to levels prior to the carbohydrate depletion treatments. Increased phosphate absorption was related to an adequate supply of reserve carbohydrates.

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#### REFERENCES

- AHMAD, R., 1963. Absorption and distribution of radioactive phosphorus and calcium in the bean plant. *Ann. Bot.* **27**: 513–515.
- ALBERDA, T., 1966. The influence of reserve carbohydrates on dry matter production after defoliation. *Proc. 10th Int. Grassld Cong.* 140–147.
- CLARK, R. B. and BROWN, J. C., 1974. Differential phosphorus uptake by phosphorus-stressed corn inbreds. *Crop Sci.* **14**: 505–508.
- CROSSETT, R. N., 1968. The site of phosphorus accumulation in maize roots. *Aust. J. biol. Sci.* **21**: 1063–1067.
- DAVIS, C. R. and WAREING, P. F., 1965. Auxin directed transport of radiophosphorus in stems. *Planta* **65**: 139–156.
- ETTER, H. M., 1967. The uptake and distribution of  $^{32}\text{P}$  by bean seedlings (*Phaseolus vulgaris*) growing at two phosphate levels and some effects of 2,4-D. *Can. J. Bot.* **45**: 1011–1017.
- HOAGLAND, D. R. and ARNON, D. I., 1950. The water culture method for growing plants without soil. *Calif. Agric. Exp. Sta. Cir.* **347**: 1–32.
- JACKSON, M. L., 1958. *Soil Chemical Analysis*. Englewood Cliffs, N.J: Prentice-Hall Inc. 498p.
- LOUGHMAN, B. C., 1966. The mechanism of absorption and utilization of phosphorus by barley plants in relation to subsequent transport to the shoot. *New Phytol.* **65**: 388–397.
- MAY, L. H. and DAVIDSON, J. L., 1958. The role of reserves in the regeneration of plants. I. Carbohydrate changes in subterranean clover following defoliation. *Aust. J. agric. Res.* **9**: 767–777.
- RUSSEL, R. S. and MARTIN, R. P., 1953. A study of the absorption and utilization of phosphate by young barley plants: I. *J. exp. Bot.* **4**: 108–127.
- SMITH, D., 1969. Removing and analysing total nonstructural carbohydrates from plant tissue. *Wisconsin Agric. Expt. Sta. Res. Report* **41**: 1–11.
- STEINKE, T. D., 1969. The translocation of  $^{14}\text{C}$ -assimilates in *Eragrostis curvula*: an autoradiographic survey. *Proc. Grassld Soc. S. Afr.* **4**: 19–34.
- STEINKE, T. D. and BOOYSEN, P. DE V., 1968. The regrowth and utilization of carbohydrate reserves of *Eragrostis curvula* after different frequencies of defoliation. *Proc. Grassld Soc. S. Afr.* **3**: 105–110.
- TARILA, A. G. I., ORMROD, D. P. and ADEDIPE, N. O., 1977. Effects of phosphorus nutrition and light intensity on growth and development of the cowpea (*Vigna unguiculata* L.). *Ann. Bot.* **41**: 75–83.